

A new species of *Wallabia* (Macropodinae: Marsupialia) from Pleistocene deposits in Mammoth Cave, southwestern Western Australia.

T. F. Flannery*

Abstract

Wallabia kitcheneri sp. nov. is described. Thus far it is known only from cranial and dental remains which have been recovered from Pleistocene deposits in Mammoth Cave, southwestern Western Australia. *Wallabia kitcheneri* is a rare element in the Mammoth Cave fauna, which seems to have been derived largely from a relatively mesic environment similar to that existing in southwestern Australia today. By inference, *W. kitcheneri* probably inhabited such an environment. The nearest relative of *W. kitcheneri* is probably *W. indra* De Vis, of the late Cenozoic of Queensland.

Introduction

The dental remains of an extinct small macropodine have long been recognized among material excavated at Mammoth Cave early this century (Merrilees 1968, Merrilees and Porter 1979). However, until now there has been no formal description of this taxon. I find it to be a species of *Wallabia*, closest to but quite distinct from *Wallabia indra* (De Vis, 1895), which is known from Pleistocene deposits in southeastern Queensland.

The Mammoth Cave fossil deposits were first investigated in detail by Glauert (1910) and their fauna has been recently reviewed by Merrilees (1979). In addition to *Wallabia kitcheneri* sp. nov. it includes *Zaglossus hacketti*, *Tachyglossus aculeatus*, *Thylacinus cynocephalus*, *Sarcophilus harrisii*, *Dasyurus geoffroyi*, *Phascogale tapoatafa*, *Antechinus flavipes*, *Sminthopsis murina*, *Perameles* sp. cf. *P. bougainville*, *Isodon obesulus*, *Potorous tridactylus*, *Setonix brachyurus*, *Macropus fuliginosus*, *Macropus eugenii*, *Macropus irma*, *Onychogalea* sp. cf. *O. unguifera*, *Protomnodon brehus*, *Simotherurus occidentalis*, *Simotherurus brownei*, *Trichosurus vulpecula*, *Pseudocheirus peregrinus*, *Thylacoleo* sp. cf. *T. carnifex*, *Zygomaturus trilobus*, *Vombatus hacketti*, *Phascolarctos cinereus*, ?*Pseudomys albocinereus*, *Pseudomys shortridgei*, *Rattus fuscipes*, a bat, several kinds of birds, lizards and frogs, and the extinct snake *Wonambi naracoortensis*. Except for the large extinct taxa, most of these species are typical of the mesic southwest of Western Australia today.

Few fossil species of *Wallabia* have been described. Bartholomai (1966) includes a redescription of the holotype of *Wallabia indra* (De Vis, 1895), and selection of a lectotype for *Wallabia vishnu* (De Vis, 1895). While both specimens lack precise locality

*The Australian Museum, 6-8 College St., Sydney, New South Wales 2000.

data, Bartholomai (1966) considers it likely that the holotype of *W. indra* was derived from the Pliocene Chinchilla Sands of southeastern Queensland, while the lectotype of *W. vishnu* derived from Pleistocene fluvial deposits on the eastern Darling Downs, southeastern Queensland. Bartholomai (1976) is a revision of the specimens of *Wallabia* found in Cenozoic deposits in Queensland, which includes all fossil types. He considers that "*Halmaturus*" *vishnu* De Vis, 1895 is a synonym of *Wallabia indra* (De Vis, 1895). Only a single extant species (*Wallabia bicolor*) is known, which differs in details of molar morphology from the extinct species. However Bartholomai (1976) considered that the major difference between *W. bicolor* and *W. indra* was size.

Dental nomenclature and enumeration follows Archer (1976, 1978). WAM is a prefix for Western Australian Museum fossil specimens.

Systematics

Superfamily Macropodoidea (Gray, 1821)

Family Macropodidae Gray, 1821

Subfamily Macropodinae (Gray, 1821)

Genus *Wallabia* Trouessart, 1904

Wallabia kitcheneri sp. nov.

(Figure 1, Table 1)

Holotype

WAM 66.9.47, fragmentary right dentary containing P₃ (in crypt), P₂, M₁₋₄, with M₅ probably in crypt also. Only the root of I₁ remains, and much of the ascending ramus is broken away.

Paratypes

WAM 66.9.29 and WAM 66.8.18, maxillary fragments containing P₃, M₂. WAM 66.8.17, left dentary fragment with P₃ (removed from crypt), posterior of P₂, M₁₋₄, probably M₅ in crypt, lacking most of I₁ crown and ascending ramus: possibly from the same individual as WAM 66.9.47. WAM 66.9.71 and WAM 66.9.72, left and right dentaries containing I₁, P₃ (in crypt), P₂, M₁₋₃ (M₄ probably in crypt). WAM 66.9.71 lacking part of ascending ramus. WAM 66.9.41, left dentary fragment containing P₂, M₁₋₂ (M₃₋₄ in crypt), lacking I₁ and diastemal area. WAM 66.9.39, right dentary fragment with partly calcified P₃ in crypt, partial M₁, M₂ (M₃₋₄ probably in crypt). WAM 66.9.40, right dentary fragment containing M₁₋₂ (M₃₋₄ probably in crypt), broken away anterior to M₁. WAM 66.9.42, left dentary fragment containing M₁, partial M₃ in crypt.

Type Locality and Age

Archer, Crawford and Merrilces (1980) consider the stratigraphy and age of the Mammoth Cave fossil fauna, and the provenance of the bones, in some detail. They consider that all of the fossil material except some much younger surficial specimens come from two deposits within the cave, termed by them the Glauert and Le Soeuf deposits, but that the great majority came from the Glauert deposit. They also note that among the thousands of bones attributed to the site held in the Western Australian

Museum, only about 50 are associated with documentary evidence stating that they originate from Mammoth Cave. The remainder are attributed as coming from that deposit largely as a matter of museum tradition. The *Wallabia kitcheneri* material unfortunately falls into this latter category. However, the specimens have calcarenite adhering to them that is extremely similar to that on other specimens known as originating from Mammoth Cave, and there is no evidence to suggest that they might have come from any other deposit.

The upper part of the Glauert deposit has two radiocarbon dates in excess of 37,000 BP, and a third date based upon a small charcoal sample from the upper part of the lower layers (but including some material from lower layers) of greater than 31,500 ybp. Thus Archer, Crawford and Merrilees (1980) suggest that the deposits are beyond the range of conventional radiocarbon dating, and (because of the bandicoot taxa present) may date to a period of intense glaciation, i.e. around 70,000 or 150,000 years ago.

Diagnosis

Wallabia kitcheneri can be distinguished from *Wallabia bicolor* on the basis of its more hypsodont lower molars that have less bowed buccal margins; lack of a well-developed preentocristid; longer anterior cingulae on lower molars; in having the protolophid narrower than the hypolophid on M/1; in its larger size, and relatively shorter premolars. It can be distinguished from *Wallabia indra* on the basis of its narrower and higher-crowned lower molars; in having the premetacristid better developed than the preprotocristid on M/1; in having narrower anterior cingulae; in that the buccal side of the molars are not as strongly bowed; and in having a markedly shorter P/3.

Etymology

Named in honour of Dr Darryl Kitchener of the Western Australian Museum, who has done so much to advance the study of mammalogy in Western Australia.

Description

Maxilla and upper cheekteeth. The only known maxillary fragments possibly represent a single individual. Unfortunately, they were not found in association with any lower dentitions. However, I consider that they are conspecific with the dentary fragments of *Wallabia kitcheneri* for the following reasons. The dimensions of the P3/ and M2/ are in accordance with the dimensions of the holotype lower dentition of *W. kitcheneri*; the maxillary teeth are morphologically compatible with the lowers assigned to *W. kitcheneri*; and there is no evidence that would suggest that two species of the genus *Wallabia* (one represented by upper dentitions only and the others by lowers only) may be present at Mammoth Cave. Thus I am satisfied that both lower and upper dentitions represent a single taxon, here designated *Wallabia kitcheneri*. In both left and right fragments the maxilla is broken away behind M2/ and just anterior to P3/. On WAM 66.8.18 what remains of the rostrum is deflected sharply ventrally from the plane of the cheektooth row, much as in the species of *Macropus*. The dental foramen is placed just above the posterior root of P3/ in WAM 66.8.18 and above the

junction of P3-M2/ in WAM 66.9.29. Insufficient of the palate is preserved to determine if palatal vacuities existed.

Both P3/'s are heavily worn. Although largely obliterated by wear, it is clear that a posterolingual cusp was present. The lingual cingulum is well-developed but low, extending anteriorly from the posterolingual cusp to terminate at a point opposite the anterior cusp of the main crest. The anterior cusp of the main crest has sharp ridges descending from it buccally, lingually and anteriorly. The rounded posterior cusp is lower than the anterior cusp, and three small cuspules with associated buccal ridgelets are present on the main crest between the anterior and posterior cusps. A small transverse enamel crest is present at the posterior edge of the tooth. Before wear, it may have formed a crest running buccally from the posterior end of the posterobuccal cusp.

Both M2/'s are so heavily worn that no occlusal structures remain. A rim of enamel *c.* 2mm high is all that remains of the crown.

Dentary and lower teeth. Unfortunately, all known dentaries of *W. kitcheneri* have the P/3 and M/5 unerupted, and thus represent young animals. The dentary shape and diastemal length are probably not representative of adults. All known dentaries are relatively gracile and have a short diastema (Figure 1). The mandibular symphysis is weakly ankylosed and extends posteriorly to just below P/2. On the most adult specimens the buccinator groove runs from below M/3 to below the posterior of M/1. On younger specimens it is restricted to below M/1. The diagastric sulcus is weakly defined, and on WAM 66.8.17 runs from below M/4 to below the anterior portion of the ascending ramus. The masseteric canal is relatively small and shallow. The mental foramen is placed just anterior to P/2 on all specimens. The coronoid process ascends nearly vertically from the cheektooth row and the condyle is subovate in shape.

Somewhat corroded I/1 crowns are preserved in WAM 66.9.72 and 66.9.71. In the former only the anterodorsal part of the crown is corroded. Prominent dorsal and ventral enamel flanges are present on the crown, while lingually an extremely thin patina of enamel is present, which gradually thickens to form the ventral flange. In overall morphology the tooth is similar to that of *W. bicolor*, but is dorsoventrally deeper.

Four complete P/2's exist, of which 3 are very similar in morphology (WAM 66.9.47, 66.9.72 and 66.9.71). In these specimens the occlusal edge is subhorizontal and three evenly-spaced cuspules are present. The anterior cusp stands slightly above the rest of the occlusal edge. The posterior cusp is slightly lower than the anterior one, and is flexed markedly lingually. WAM 66.9.41 differs from the above specimens in that the anterior cusp is well-separated from the rest of the occlusal edge by a groove *c.* 1.0mm deep. The groove separating the posterior and median cusps also seems better defined.

Four P/3's are available for examination (WAM 66.9.72, 66.9.47, 66.9.39 and 66.8.17) of which only one (WAM 66.8.17) has been completely removed from the crypt. Of the others, only their buccal surfaces can be seen. Where discernable, all specimens consist of a single, high and short crest ornamented by an anterior and posterobuccal cusp, with two smaller cuspules placed between them. All cuspules are

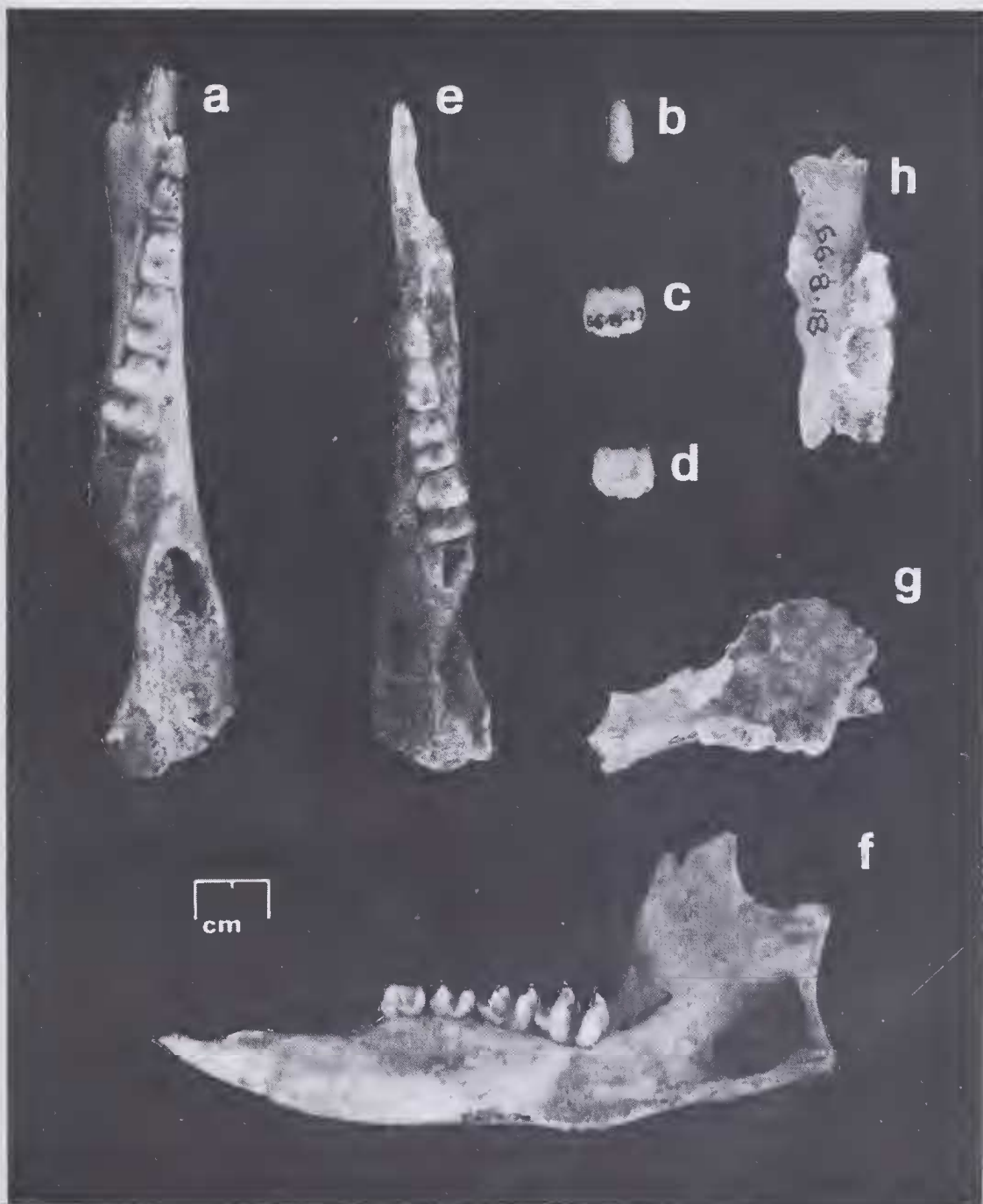


Figure 1: a, occlusal view of right dentary of WAM 66.9.47 (holotype); b-d, occlusal, buccal, lingual views of right P 3 (removed from the crypt) of WAM 66.8.17 (paratype); e-f, occlusal and lingual views of the left dentary of WAM 66.9.72 (paratype); g-h, buccal and occlusal views of the left maxillary fragment WAM 66.8.18 (paratype). All of *Wallabia kitcheneri* sp. nov.

Table 1 Dental measurements (in mm) of all known specimens of *Wallabia kitcheneri* sp. nov.

			Length	Anterior width	Posterior width
WAM66.8.17	Left dentary	M/1	6.4	3.8	4.6
		P/3	8.6	3.1	3.7
		M/2	7.5	5.2	5.5
		M ₁ 3	8.9	6.2	6.5
		M ₁ 4	11.4	7.4	7.3
WAM66.9.47	Right dentary (? same individual as WAM66.8.17)	P/2	6.2	2.7	3.3
		M/1	7.6	3.7	4.4
		M/2	7.6	5.0	5.5
		M ₁ 3	9.3	6.3	6.4
		M 4	11.5	7.4	7.4
WAM66.9.71	Left dentary	P/2	6.3	2.7	3.2
		M/1	7.2	3.5	4.4
		M 2	8.2	5.2	5.3
		M ₁ 3	10.0	6.4	-
WAM66.9.72	Right dentary (? same individual as WAM66.9.71)	P/2	6.2	2.4	3.1
		M ₁ 2	8.0	5.2	5.3
		M ₁ 3	9.8	6.5	-
WAM66.9.41	Left dentary	P/2	6.1	2.8	3.7
		M 1	6.9	3.5	4.2
		M ₁ 2	8.2	5.0	5.4
WAM66.9.40	Right dentary (? same individual as WAM66.9.41)	M 1	7.0	3.5	4.3
		M ₁ 2	8.3	4.8	5.3
WAM66.9.39	Right dentary	M 2	8.6	5.6	5.8
WAM66.9.42	Right dentary	M 1	7.5	4.2	4.9
WAM66.8.18	Left maxilla	P3 ₁	10.9	4.9	5.8
		M2 ₁	-	7.1	7.4
WAM66.9.29	Right maxilla (? same individual as WAM66.8.18)	P3 ₁	10.6	4.0	5.9
		M2 ₁	-	7.0	-

subequal in height. The short, high crown of P/3 in *W. kitcheneri* is markedly different from anything seen in closely related taxa, which usually have lower, more elongated P/3's.

All known specimens of the lower dentition of *W. kitcheneri* include an M/1, and some morphological diversity is apparent in the sample. However, all are similar in having the protolophid markedly narrower than the hypolophid. The anterior cingulum is narrow and elongate. The moderately well-developed cristid obliqua runs from the hypoconid apex to the rear face of the protoconid. The metaconid is taller than the protoconid. A strong paracristid and weaker premetacristid define the buccal

and lingual margins of the anterior cingulum. These structures are usually straight, but in WAM 66.9.42 they are kinked towards each other near their midpoints. A well-developed premetacristid runs from the apex of the metaconid along the lingual edge of the tooth into the interlophid valley. A straight preentocristid runs from the entoconid along the lingual margin of the tooth to the interlophid valley. The rear face of the hypolophid is vertically oriented and unornamented.

All dentary specimens of *W. kitcheneri* except WAM 66.9.42 include M/2. The hypolophid and protolophid are subequal in width and height. The anterior cingulum is narrow, relatively shorter than in M/1 and is low. Its buccal margin is convex when viewed from above, and its lingual margin is straight. The paracristid is kinked, running anterolingually from the apex of the protoconid then turning gently anteriorly to join the anterior cingulum. A small lingual fossette is present lingual to the paracristid. A premetacristid runs anteriorly from the apex of the metaconid along the lingual edge of the tooth, but in most specimens it fails to contact the anterior cingulum. The cristid obliqua is kinked in a similar fashion to the paracristid, running from the apex of the hypoconid to about one-third of the way from the buccal edge of the rear face of the protolophid. Thus it is placed further lingually than on M/1. The rear face of the hypolophid is vertically oriented and unornamented. The M/3 differs from M/2 in being larger, and in having a more pronounced convex buccal margin to the lophids. The M/4 differs from M/3 in being larger and in having more markedly convex molar margins. The M/5 is unknown.

Discussion

The reasons for assigning the Mammoth Cave material described herein to the genus *Wallabia*, rather than some other macropodine genus, is as follows: the species of *Wallabia* (including *W. kitcheneri*) differ from the species of *Macropus*, *Onychogalea* and *Petrogale* in possessing much less hypsodont molars and in lacking an arched alveolar margin on the dentary (Dawson and Flannery 1985); they differ from species of *Dorcopsis*, *Dorcopsulus*, most *Dendrolagus*, *Dorcopsoides* and *Prionotemnus* in having a well-developed protolophid on M/1. They differ from the species of *Protemnodon*, *Galanarla*, *Dorcopsoides* and *Prionotemnus* in lacking posterior cingulae on the lower molars; from species of *Lagorchestes* in having much narrower anterior cingulae in lower molars, from *Baringa* in lacking a crest on the rim of the masseteric foramen, from *Kurrabi* species in having a fenestrate palate; from *Thylogale* and *Setonix* species in being larger; and from *Setonix* in having more elongate molars.

With only three species in the genus *Wallabia*, and with no clear plesiomorphic outgroup, it is difficult to speculate upon relationships. Bartholomai (1976) clearly envisaged *Wallabia vishnu* as the ancestor to *W. bicolor*. However, *W. bicolor* possesses a number of dental peculiarities that are not seen in *W. vishnu*. These include presence of an accessory midlink on upper molars, and a secondary cristid obliqua on lowers. Furthermore, remains of *W. bicolor* dating to the late Pliocene from Victoria

have recently been discovered (M. Whitlaw pers. comm.), making an ancestor-descendant relationship with *W. vishnu* highly unlikely. Overall, the molar morphology of *W. vishnu* and *W. kitcheneri* are more similar to each other than either is to *W. bicolor*, and this may suggest that they are close relatives.

An understanding of the biota from which the Mammoth Cave fossil assemblage was derived is hampered by lack of data about where individual specimens were obtained. Archer, Crawford and Merrilees (1980) note that the bulk of the bones came from two locations within the cave. Unfortunately, the temporal and geographic relationships of these deposits are unknown, and some specimens may have been from recent surficial deposits. The *Wallabia kitcheneri* material clearly does not fall into this last category, as some specimens are cemented into calarcnite, but it is unclear if they came from both, or only one of the older deposits. Even given these difficulties however, a little can be said regarding the ecological significance of the remains.

The Mammoth Cave fauna material can be divided into three groups on the basis of extinction patterns; 1) taxa that became extinct throughout Australia in the late Pleistocene; 2) taxa that became extinct in the southwest, but which survived (or at least near relatives survived) in eastern Australia; and 3) taxa still existing in Western Australia. *Wallabia kitcheneri* clearly falls into the second category. It, along with *Vombatus hacketti* and *Phascolarctos cinereus* either still exist or have closely related species in eastern Australia. Interestingly, all of the surviving eastern species inhabit eucalypt forest, although some can be found in other habitats as well. The extinction of these species or their near relatives in southwestern Western Australia, but not in the east, may be due to differing climatic and vegetational histories of the two areas.

Acknowledgements

I wish to warmly thank Dr Ken McNamara, Curator of fossils for his extended loan of the material described herein, and his forbearance with the long delays involved in completing this manuscript. Mr K. Aplin engaged in useful discussions of the relationships of the species of *Wallabia* which contributed to this work.

References

- Archer, M. (1976). Phaseolaretid origins and the potential of the selenodont molar in the evolution of diprotodont marsupials. *Mem. Qd Mus.* 17:367-371.
- Archer, M. (1978). The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Mem. Qd Mus.* 18:157-164.
- Archer, M., Crawford, I.M. and Merrilees, D. (1980). Incisions, breakages and charring, some probably Man-made, in fossil bones from Mammoth Cave, Western Australia. *Alcheringa* 4:115-132.
- Bartholomai A. (1966). The type specimens of some of De Vis' species of Macropodidae. *Mem. Qd Mus.* 14:115-125.
- Bartholomai, A. (1976). The genus *Wallabia* Trouessart (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Mem. Qd Mus.* 17:375-377.

- Dawson, L. and Flannery, T.F. (1985). Taxonomic and phylogenetic status of living and fossil kangaroos and wallabies of the genus *Macropus* Shaw (Macropodidae: Marsupialia) with a new subgeneric name for the large wallabies. *Aust. J. Zool.* **33**:473-498.
- Glauert, L. (1910). The Mammoth Cave. *Rec. Western Aust. Mus.* **1**:11-36.
- Merrilees, D. (1968). Man the destroyer: late Quaternary changes in the Australian marsupial fauna. *J. Roy. Soc. Western Aust.* **51**:1-24.
- Merrilees, D. (1979). The prehistoric environment in Western Australia. *J. Roy. Soc. Western Aust.* **62**:109-128.
- Merrilees, D. and Porter, J.K. (1979). Guide to the Identification of Teeth and Some Bones of Native Land Mammals Occurring in the Extreme Southwest of Western Australia. Western Australian Museum, Perth.